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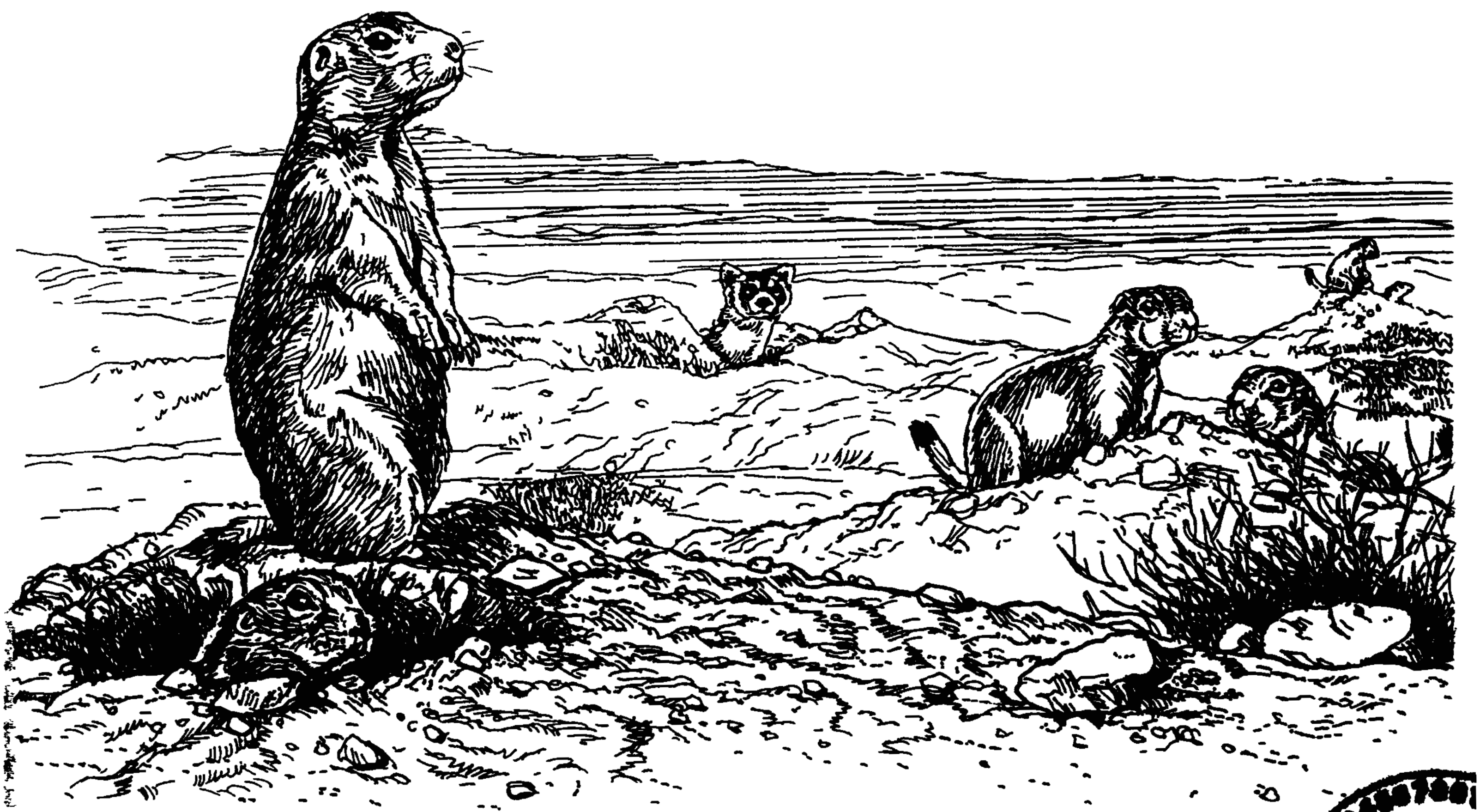

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Effects of Prairie Dogs on Physical and Chemical Properties of Soils

by

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Abstract. The literature reveals little quantifying data about the effects of prairie dogs (*Cynomys* spp) on physical and chemical properties of soils Black-tailed prairie dogs (*C ludovicianus*) move more soil material and live in larger and denser social groups than other species of prairie dogs. They are, therefore, more likely to alter soils in their habitat. Prairie dogs alter species composition and biomass of plants litter, and bare ground in their colony areas These alterations, in addition to the direct effects of burrowing, may be expected to change soil properties permanently In general, prairie dogs contribute to patchiness or diversity of the environment. Rates of soil mixing by prairie dogs are more rapid than normal rates of soil formation. On sodium affected soils and on shallow soils activities by prairie dogs tend to increase plant biomass. Where the prairie dogs bring subsoil with salts and carbonates to the surface of a noncalcareous soil, productivity tends to decrease

Key words: Soil mixing rates, pedoturbation, *Cynomys* spp

Much of the literature on the effects of prairie dogs (*Cynomys* spp.) on the properties of the soil is about the building of mounds by the black-tailed prairie dog (*C. ludovicianus*, Koford 1958, Sheets et al. 1971, Potter 1980; White and Carlson 1984, Cincotta 1985, 1989, Carlson and White 1987, 1988). The white-tailed prairie dog (*C leucurus*) has been studied less intensively by pedologists, perhaps because it does not build large mounds (Koford 1958; Tileston and Lechleitner 1966, Clark 1971, 1977, Stromberg 1978, Flath and Paulick 1979, Schloemer 1991) Most of the literature on the effects of prairie dog activities on soil properties is about the effects of pedoturbation or soil mixing from the burrowing of these animals Since Thorp (1949) calculated that prairie dogs (species not given) built 54 6 metric tons of mound material per hectare and converted the surface soils on one-third of the Akron, Colorado, Dryland Experiment Farm from silt loam to loam texture, there has been much interest in calculating mixing rates attributable to rodents. White and Carlson (1984) suggest that many of these attempts need to be viewed with caution. Although mixing of subsoil and topsoil layers has been estimated by numerous authors, documentation of short- and long-term effects of prairie dog activity on the chemistry and morphology of soils is scarce Documentation is particularly scarce of the effects of prairie dog induced changes in plant physiology and community structure on soil properties. The literature also does not address the persistence of prairie dog induced changes in soils after abandonment of the prairie dog town

Literature Review

Koford's (1958) monograph provides an extensive discussion of the interrelations between prairie dogs, the soil, plant communities, and livestock. He lists additions of organic matter and nutrient salts, improvement of soil structure, and increased water infiltration as beneficial effects of prairie dog activity. Koford calculated that 12 burrows have a volume of 2.7 m^3 (95 cubic feet) and represent the removal of 3.63 metric tons (4 tons) of soil to the surface. He considered this a reasonable estimate for 0.4 ha of an established prairie dog town. White and Carlson (1984) calculated that 550 years are required to cover a hectare with mounds and that 8,800 years are required to create a hectare of burrows, assuming the prairie dogs constructed new burrows each year, which they do not do. They concluded that the effect of soil mixing by rodents may be greatly exaggerated in the literature. Black-tailed prairie dogs mix soil excavated from their burrows with surface soil gathered from the area surrounding their burrows to create a large compact mound (Koford 1958, Smith 1958). The mounds of white-tailed prairie dogs, however, are simply a pile of subsoil removed from the burrows (Clark 1971). The black-tailed prairie dog builds larger, more complex burrows (Tileston and Lechleitner 1966, Sheets et al. 1971) and probably mixes greater volumes of soil over time. However, Clark (1971) concluded that there was no species-specific pattern of tunnel excavation. Seemingly, the burrow system is continuously enlarged and modified while it is occupied (Longhurst 1944). Burrows occupied by female white-tailed prairie dogs with litters are enlarged throughout the period when the young are raised (Flath and Paulick 1979). An additional consideration is the enlargement of prairie dog burrows by badgers (*Taxidea taxus*). Campbell and Clark (1981) reported that 10–27% of the burrows on the sites they studied had been enlarged by badgers in pursuit of prairie dogs.

Potentially harmful effects of prairie dogs on soils include accelerated erosion because of increased bare ground from removal of vegetation (Koford 1958) and the calcification of noncalcareous surface horizons from the mixture of carbonate ($CaCO_3$) rich subsoil material. As an example of the latter effect, soils mapped on the north flank of Sheep Mountain in Albany County, Wyoming, are a complex of Haplargids and Calciorthids where the rodents converted appreciable areas of soils with noncalcareous argillic horizons to soils that are now calcareous throughout the profile (Soil Conservation Service, Casper, Wyoming, unpublished data).

Prairie dogs apparently prefer flat open areas and often colonize old fields (Longhurst 1944, Koford 1958, Dalsted et al. 1981). Dalsted et al. (1981) listed four characteristics of sites that black-tailed prairie dogs prefer:

1. deep soils free from excessive stoniness,
2. minimal flooding hazard,
3. moderate or better productivity of soils, and
4. slopes of less than 9%.

Prairie dogs also dig, however, in gravelly soils and in soils of extremely high density (so high that digging is difficult for a human with a steel shovel), and on soils with only sparse vegetation. White-tailed prairie dogs and Gunnison's prairie dogs (*C. gunnisoni*) inhabit more steeply sloping sites than black-tailed prairie dogs (Longhurst 1944, Koford 1958, Fitzgerald and Lechleitner 1974). In large contiguous towns, the burrows are unevenly spaced, apparently in response to food and soil conditions (Sheets et al. 1971). Density and distribution of prairie dogs are more likely controlled by available food than by edaphic conditions, with the exception of the exclusion of rodents by high water tables (Koford 1958).

Carlson and White (1987) provide detailed data on soil chemistry (pH, N, P) and soil color in two black-tailed prairie dog mounds that they transected in South Dakota. They reported enrichment in P but concluded that effects by prairie dogs on soils were mostly confined to the mound area itself. Cincotta (1985) reported differences in soil organic matter, available phosphorus, and available nitrogen in black-tailed prairie dog towns of varying ages and in adjacent unoccupied areas. Early in the year, available P and N were higher in soils in the prairie dog town than in the adjacent undisturbed soil. Potter (1980) found higher organic matter contents in crater mounds of the black-tailed prairie dog than in dome mounds and in intermound topsoil. Tadzhiyev and Odinoshoyev (1987) reported similar changes as a result of burrowing activities of marmots (*Marmota caudata* Leoff) in the Pamirs where the rodents excavated 6–8 burrows/ha. The marmots increased soil pH in the mounds by bringing carbonate-rich subsoil to the surface, brought stones to the surface, decreased soil humus (except in Alpine desert where it increased), and altered the distribution of N and P in the soil profiles Carlson and White (1988) reported increases in pH in the mounds but not in the nonmound areas in a black tailed prairie dog town

Because more soil area is affected by the mound than by the burrow (White and Carlson 1984), changes in soil chemistry probably reach beyond the area directly excavated by the animals Schloemer (1991) investigated white tailed prairie dog colonies on soils derived from a Cretaceous age marine shale in the Shirley Basin in Wyoming He reported that prairie dog colonies can be located visually from distances of 100 m or more because of the enhanced vigor of sagebrush (*Artemisia tridentata*) in the colony area The dominant soils of this landscape have dense subsoils of clay accumulation and appreciable sodium (Na) on the exchange complex (natric horizons, Soil Survey Staff 1987) and subsurface segregation of carbonates, gypsum, and salts He attributed the greater productivity of sagebrush in the colony area to several mechanisms

1 an increase in macroporosity of the soil,
2 the substitution of calcium for sodium on the exchange complex as a result of the transfer of gypsiferous subsoils to the soil surface,
3 deeper penetration of precipitation as a result of increased electrolyte content of infiltrating rain water, and
4 incorporation of organic materials into the soil as plant parts and feces

The Natragids (soil taxonomy names after Soil Survey Staff 1987) in the Shirley Basin are representative of one type of soil that probably responds positively to pedoturbation. Farmers commonly amend such soils with gypsum and manure to improve infiltration of water

The literature on the effects of prairie dogs on vegetation is voluminous and dates to Merriam's (1901) calculation that the occupants of one large colony of black-tailed prairie dogs in Texas consumed enough forage each year to support 1 6 million cattle Recent literature reflects greater realism and consists of reports on the diverse effects on plant community structure, plant physiology, and biomass (Clark and Kinker 1970; Bonham and Lerwick 1976, Bonham and Hannan 1978, Klatt and Hein 1978, Coppock et al. 1983; Ursek 1985, 1987, Agnew et al 1986) Authors cite prairie dog-induced changes in plant vigor, species composition, plant height, plant nutrient content, biomass and reproduction success, and litter and bare ground characteristics Virtually all of these changes can be expected to affect soil carbon storage, nutrient cycles, chemistry, and morphology Agnew et al (1986) reported that prairie dog activity contributed to species richness and to patchiness of the ecosystem This ecosystem diversity is exploited by other species of wildlife including bison (*Bison bison*), pronghorns (*Antilocapra americana*), black-footed ferrets (*Mustela nigripes*), and a host of birds, small mammals, and insects (Wilcomb 1954, Coppock et al 1983, Agnew et al 1986)

Age and Profile Characteristics of Soils in the High Plains and Wyoming Basins

The age of soils in the high plains and basins of Wyoming is highly variable, soils on steep south facing slopes are kept perpetually young by erosion. In contrast, soils on many flat stable surfaces date to the Pleistocene and some perhaps to the Tertiary period (Mears 1991) Even in the mountains of Wyoming under high rainfall soils developed on geomorphic surfaces younger in age than Bull Lake (~140,000 years before present [YBP]) typically have not formed noncalcareous subsurface horizons of clay accumulation (argillic horizons) An exception is the coarse-textured parent materials where some soils of post-Pinedale age (~15,000 YBP) may have minimal argillic horizons (Munn 1987) Because many soils on the high plains and intermountain basins are Pleistocene relicts that developed under other than contemporary climatic conditions, burrowing by prairie dogs may effect permanent changes in soil chemistry and morphology

The Laramie Basin in south central Wyoming is typical of the intermountain basins in the northern Rockies. In the Laramie Basin, soils range in age from young soils on the modern floodplain and eroding slopes to old mature soils on alluvial terraces that are at least 2 million years old. The older surfaces typically are occupied by Haplargids and Paleorthids (Soil Conservation Service, Casper, Wyoming, unpublished data) A representative soil horizon sequence of the Haplargids is E (thin leached surface), Bt (clay accumulation), Bk (carbonate accumulation), By (gypsum accumulation), and Bz (salt accumulation, horizon nomenclature is after Soil Survey Staff 1981) On old alluvial surfaces, the soils show the upward fining characteristic of alluvium–loam or clay loam textures over gravelly sands Many of the older soils in the Laramie Basin (and other Wyoming basins) show evidence of cryoturbation during periods of perma frost (Mears 1981, Munn 1987). Complexes of soils occur where Haplargids are apparently converted to Calciorthids (Table 1) as a result of mixing by rodents—both prairie dogs and the Richardson's ground squirrel (*Spermophilus richardsoni*) and an apparent decrease in effective precipitation since the soils originally formed. After excavation of subsoil carbonates to the soil surface by rodents, present day precipitation is insufficient to leach the carbonates from the surface tier. Mixing by the rodents also distributes gravel from the subsoil throughout the fine-textured surficial layers. The conversion of Haplargids to Calciorthids can profoundly reduce vegetative biomass. For example, the Dalquist series (Borollic Haplargid) has a rated productivity of 1,300 kg / ha compared with 450 kg / ha of the Browtine series (Borollic Calciorthid, Soil Conservation Service).

Prairie dogs frequently dig through the solum of the soil on sideslopes and bring fragments of soft bedrock (often shale or sandstone) to the surface where its weathering is accelerated. Virtually all exposures of soil profiles in grasslands reveal krotovinas, the casts of rodent burrows. These features are assumed by pedologists to persist for long periods (hundreds of years), but their persistence is not well documented (Borst 1968, Allgood and Gray 1974). Observations of the effects of prairie dog removal on vegetation (Bishop and Culbertsen 1976, Uresk 1985, 1987) have generally been conducted for too short a time to allow understanding of the long term effects of burrowing on soil properties.

Mixing of Soil by Prairie Dogs

Because of the wide range of burrow densities (Table 2) and burrow and mound volumes (Table 3) any calculation of possible turnover or mixing rates by prairie dogs must be prefaced by a careful listing of assumptions. White and Carlson (1984) used 62 burrows per ha, a burrow diameter of 15 cm, and an average mound diameter of 0.6 m. They calculated that prairie dogs could create a hectare of mounds in 550 years and a hectare of burrows in 8,800 years if the animals constructed new burrows each year. This led them to conclude that the effect of the rodents on mixing soil materials described in the literature may often be exaggerated. However, compared with the normal time scale of soil formation, such turnover rates are quite rapid.

For a representative calculation of mixing rates in a white-tailed prairie dog colony I used 20 burrows / ha, an average burrow volume of 0.15 m^3, and a mound diameter of 0.5 m for non-maternity burrows and 1.0 m for maternity burrows. Ten percent of the burrows were assumed to be maternity burrows with a volume of 0.30 m^3. Approximately 20% of the burrows were presumed to be excavated by badgers to four times their original volume (0.60 m^3). Finally, new burrow

Table 1. *Comparison of Dalquist (Haplargid) and Browtine (Calciorthid) soil profiles in a prairie dog affected soil complex, Albany County, Wyoming (Soil Conservation Service 1988).*

Horizon	Depth (cm)	Color 10YR hue[a] (value / chroma)	Fine earth textural class	Coarse fragments (%)	$CaCO_3$ (%)	Effervescence	pH
Dalquist							
A	0–5	6 / 2 d, 4 / 2 m	sl	50	—	—	7.0
BA	5–13	5 / 3 d, 4 / 3 m	scl	50	—	—	7.2
Bt	13–38	5 / 4 d, 4 / 3 m	scl	45	—	—	7.2
Bw	38–50	6 / 6 d, 5 / 4 m	scl	40	6	discontinuous	7.5
Bk1	50–63	6 / 4 d, 5 / 4 m	sl	85	35	violent	8.6
Bk2	63–150	6 / 4 d, 5 / 4 m	sl	55	8	strong	8.2
Browtine[b]							
A	0–8	5 / 3 d, 4 / 3 m	sl	40	7	strong	8.0
AB	8–22	6 / 3 d, 5 / 3 m	sl	55	18	violent	8.2
Bk1	22–35	8 / 2 d, 7 / 3 m	sl	45	37	violent	8.4
Bk2	35–78	8 / 2 d, 7 / 3 m	l	75	36	violent	8.6
C	78–150	6 / 6 d, 5 / 6 m	sl	80	7	strong	8.2

[a] Color: d = dry, m = moist
[b] 10%–50% surface cover of pebbles, cobbles, and stones

Table 2 *Average densities of burrows by four species of prairie dogs*

Species of prairie dog	Burrow density (burrows per hectare)		Source	Comments
Gunnison s[a]	57		Fitzgerald and Lechleitner (1974)	Only 10% had mounds
Gunnison s	2–5	(sagebrush)	Longhurst (1944)	—
	37–49	(fields)		
	74	(maximum)		
Black-tailed[b]	3		Sheets et al (1971)	43 ha colony not evenly distributed, 4 1 animals / burrow
Black tailed	—		Smith (1958)	55–56 animals / ha
White-tailed[c]	—		Flath and Paulick (1979)	Mounds 6 m in diameter, 57 cm tall
White-tailed	9	(grass)	Clark (1977)	Laramie, Wyoming area
Black tailed (?)	42		Thorp (1949)	Species unspecified
Black-tailed	247		Koford (1958)	Fed by tourists
Black tailed	54–128		Koford (1958)	15 / ha in a new dog town
White-tailed	54		Tileston and Lechleitner (1966)	—
Black tailed	103		Tileston and Lechleitner (1966)	—
Black-tailed	84		Bishop and Culbertsen (1976)	—
White-tailed	25	(9–129)	Campbell and Clark (1981)	—
Black tailed	21	(11–67)	Campbell and Clark (1981)	—
Utah[d]	—		Collier and Spillett (1972)	6 animals / ha
White-tailed	0 7		Stromberg (1978)	—
Black-tailed	0 7–3 7		Stromberg (1978)	—
Black-tailed	8 9		King (1955)	—
White-tailed	59		Clark (1971)	Laramie area

[a] *Cynomys gunnisoni*
[b] *C ludovicianus*
[c] *C leucurus*

Table 3 *Volume of prairie dog burrows and mounds*

Burrow (m^3)	Mound (m^3)	Source	Comments
0 14, 0 23	—	Koford (1958)	Data from Merriam (1901) and Fish and Wildlife Service
0 22	—	Wilcomb (1954)	—
—	0 023	White and Carlson (1984)	Model based on a mound 0 6 m in diameter and 0.3 m high
—	0 014 0 028	Clark (1977)	Calculated from mound dimensions
0 04 0 38, (0 15 av)	—	Sheets et al (1971)	Calculated for burrows without chambers, 12 cm diameter
—	6 4	Thorp (1949)	Largest mound
0 02 0 10, (0 05 av)	—	Stromberg (1978)	Calculated for burrows without chambers, 12 cm diameter
0 12	—	Smith (1958)	Calculated for burrows without chambers 12 cm diameter
—	5 4	Flath and Paulick (1979)	Largest mound
—	0 13	Fitzgerald and Lechleitner (1974)	Largest mound
—	4 37	Carlson and White (1987)	Large mound was 14 6 m diameter by 0 67 m high

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svstems were assumed to be constructed every 10 years and the depth of the burrows 1 5 m

Based on the described assumptions prairie dogs produced 5 1 m^2 of mound basal area, which if renewed every 10 years covered a hectare in 19 600 years Mixing of the 1 5 m of soil by the rodents occurred in 29 760 years during continu ous occupation of the colony This estimate is low because the rodents were redigging some of the same soil material each time Because of their usual greater burrow density black tailed prairie dogs mixed soil at a greater rate (perhaps as much as five fold) Episodic depopulation of the colony slowed the rate of change However, even if the final estimate is doubled or tripled (100 000 years for soil mixing and 20,000 years for coverage of the ground with subsoil [mound] material), the time period is still relatively short compared with the age of many soils in the intermountain basins of Wyoming and the high plains

Horizons of alluvial clay accumulation on Pleis tocene surfaces are probably relicts in soils with more than 15% clay in the surface (E) horizons under the present climate in Wyoming's basins (<35 cm annual precipitation) Textural stratifica tion with depth is a relict condition inherited from the parent material in soils developed in alluvium and in soils developed in interbedded sedimentary rocks of contrasting texture (e g , sandstone over shale) In these situations admixture of calcare ous and gypsiferous subsoil to the surface of the soil creates a permanent change in soil chemistry, and admixture of subsoil materials to surface ho rizons permanently changes soil texture These changes cause a patchiness in the vegetation on the site until virtually all of the site is affected by rodent activity Despite the apparently irre versible nature of some of these effects prairie dog colonies are irregularly distributed in the land scape and their populations fluctuate markedly over time The net effect of their activity is to increase diversity in the environment—diversity in soil properties and in plant community charac teristics

Where goals of management call for expansion of existing prairie dog towns or reintroduction of prairie dogs to sites from which they were elimi nated in the past prediction of the probable effects of prairie dog burrowing on soils and associated vegetation mav be desirable In the intermountain basins of the Rocky Mountains and adjacent high plains major changes in plant growth will prob ably occur as a result of burrowing by prairie dogs These changes are expected

1 on alluvial soils with abrupt contrast in texture between horizons (loamy layers over gravelly layers)
2 on Haplargid profiles where noncalcareous sur face layers (E and Bt horizons) overlie carbon ate and salt rich Bk By and Bz horizons
3 on Natragid profiles where the sodium affected Btn horizon is underlain by gypsum (By horizon),
4 on shallow Torriorthents (young poorly devel oped soils) where soft bedrock is brought to the surface and weathering accelerated and
5 on favored sites where burrow density is greatest

Least affected will be soils of extremely uniform texture (e g , Psamments) and soils with very thick A horizons (pachic and cummulic Subgroups of Mollisols) on sites with high water tables (aquic Suborders and Subgroups)

References

Agnew W D W Uresk and R M Hansen 1986 Flora and fauna associated with prairie dog colonies and adja cent ungrazed mixed grass prairie in western South Dakota Journal of Range Management 39 135–139

Allgood F P and F Gray 1974 An ecological interpreta tion for small mounds in landscapes of eastern Okla homa Journal of Environmental Quality 3 37–41

Bishop N G and J L Culbertsen 1976 Decline of prairie dog towns in southwestern North Dakota Journal of Range Management 29 207–220

Bonham C D and J S Hannan 1978 Blue grama and buffalograss patterns in and near a prairie dog town Journal of Range Management 31 63–65

Bonham C D, and A Lerwick 1976 Vegetation changes induced by prairie dogs on shortgrass range Journal of Range Management 29 221–225

Borst G 1968 The occurrence of crotovina in some southern California soils Transactions of the Ninth International Congress of Soil Science 2 19–27 Ade laide Australia

Campbell T M III and T W Clark 1981 Colony char acteristics and vertebrate associates of white tailed and black tailed prairie dogs in Wyoming American Midland Naturalist 105 269–276

Carlson D C and E M White 1987 Effects of prairie dogs on mound soils Soil Science Society of America Journal 51 389–393

Carlson D C and E M White 1988 Variations in surface laver color texture pH and phosphorus con tent across prairie dog mounds Soil Science Society of America Journal 52 1758–1761

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Cincotta, R. P. 1985 Habitat and dispersal of black-tailed prairie dogs in Badlands National Park. Ph.D dissertation, Colorado State University, Fort Collins 60 pp

Cincotta, R. P. 1989 Note on mound architecture of the black-tailed prairie dog Great Basin Naturalist 49 621–623

Clark, T. W 1971 Notes on white-tailed prairie dog (*Cynomys leucurus*) burrows Great Basin Naturalist 31 115–125

Clark, T W 1977 Ecology and ethology of the white-tailed prairie dog (*Cynomys leucurus*) Milwaukee Public Museum Publications in Biology and Geology 3 97 pp

Clark, T. W, and J W Kinker 1970 Some prairie dog range relationships in the Laramie Plains, Wyoming Wyoming Range Management 281 40–51

Collier, G D., and J J Spillett. 1972 Status of the Utah prairie dog Utah Academy of Sciences 49.27–39

Coppock, D L., J K. Detling, J E Ellis, and M. I Dyer. 1983 Plant-herbivore interactions in a North American mixed-grass prairie I. Effects of black-tailed prairie dogs on interseasonal aboveground plant biomass and nutrient dynamics and species diversity Oecolgia 56 1–9

Dalsted, K. J, S Sather-Blair, B K. Worcester, and R. Klukas. 1981 Application of remote sensing to prairie dog management Journal of Range Management 34:218–223

Fitzgerald, J P, and R. R Lechleitner. 1974 Observations on the biology of Gunnison's prairie dog in central Colorado American Midland Naturalist 92 146–163

Flath, D L., and R. K. Paulick. 1979 Mound characteristics of white-tailed prairie dog maternity burrows American Midland Naturalist 102.395–398

King, J A. 1955 Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contributions from the Laboratory of Vertebrate Biology of the University of Michigan 67 123 pp

Klatt, L. E, and D Hein. 1978 Vegetative differences among active and abandoned towns of black-tailed prairie dogs (*Cynomys ludovicianus*) Journal of Range Management 31.315–317

Koford, C B. 1958 Prairie dogs, whitefaces and blue grama. Wildlife Monographs 3. 78 pp

Longhurst, W 1944 Observations on the ecology of the Gunnison prairie dog in Colorado Journal of Mammalogy 25:24–36

Mears, B, Jr 1981 Periglacial wedges and the late Pleistocene environment of Wyoming's intermontane basins Quaternary Research 15 171–198

Mears, B Jr 1991 Laramie Basin. Pages 418–427 *in* R. B Morrison, editor Quaternary nonglacial geology Conterminous U.S Geological Society of America, Decade of North American Geology Series, Boulder, Colo.

Merriam, C H. 1901 The prairie dog of the Great Plains U S Department of Agriculture Yearbook.257–270.

Munn, L. C 1987. Soil genesis associated with periglacial ice wedge casts, southcentral Wyoming. Soil Science Society of America Journal 51.1000–1004

Potter, R. L. 1980 Secondary successional patterns following prairie dog removal on shortgrass range. M.S thesis, Colorado State University, Fort Collins. 165 pp.

Schloemer, R. D 1991 Prairie dog effects on vegetation and soils derived from shale in Shirley Basin, Wyoming. Ph.D dissertation, University of Wyoming, Laramie 158 pp

Sheets, R. G, R. L Linder, and R. B Dahlgren. 1971 Burrow systems of prairie dogs in South Dakota. Journal of Mammalogy 52.451–453

Smith, R. E. 1958 Natural history of the prairie dog in Kansas Museum of Natural History and State Biological Survey University of Kansas Miscellaneous Publication 16 1–36

Soil Survey Staff. 1981 Soil survey manual. Chapter 4 (430-v-SSm) U.S. Department of Agriculture 503 pp

Soil Survey Staff. 1987 Keys to soil taxonomy. 4th. edition. Soil Management Support Services, Technical Monograph 6 U.S Department of Agriculture Blacksburg, Va.

Stromberg, M. R. 1978 Subsurface burrow connections and entrance spatial pattern of prairie dogs Southwestern Naturalist 23 173–180

Tadzhiyev, R., and A. Odinoshoyev 1987 Influence of marmots on soil cover of the eastern Pamirs. (Translated from) Pochvovedeniye 1 63–71.

Thorp, J 1949 Effects of certain animals that live in soils Scientific Monthly 68·180–191

Tileston, J V., and R. R. Lechleitner. 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. American Midland Naturalist 75:292–316

Uresk, D W 1985 Effects of controlling black-tailed prairie dogs on plant production. Journal of Range Management 38:466–468.

Uresk, D. W 1987 Relation of black-tailed prairie dogs and control programs to vegetation, livestock and wildlife. Pages 312–323 *in* J L. Capinera, editor. Integrated pest management on rangeland. A shortgrass prairie perspective. Westview Press, Boulder, Colo.

White, E M., and D. C Carlson. 1984 Estimating soil mixing by rodents. Proceedings of the South Dakota Academy of Science 63.34–37

Wilcomb, M. J 1954 A study of prairie dog burrow systems and the ecology of their arthropod inhabitants in central Oklahoma. Ph.D dissertation, University of Oklahoma, Norman. 158 pp

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